OBSERVATIONS ON THE POSTCRANIAL MORPHOLOGY, ONTOGENY AND PALAEOBIOLOGY OF *SCLEROCEPHALUS HAEUSERI* (AMPHIBIA: ACTINODONTIDAE) FROM THE LOWER PERMIAN OF SOUTHWEST GERMANY

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The temnospondyl amphibian *Sclerocephalus*, in particular its postcranial anatomy, is described in 4 ontogenetic stages: larval, juvenile, adult and late adult. Some specimens preserve stomach contents, consisting of paramblypterid fishes and small amphibians (*Micromelerpeton*, *Apateon*). In one specimen, the remains of a small *Sclerocephalus* were found. Larval and juvenile individuals probably lived in a different habitat than adult and late adult ones. In the juvenile, adult and late adult stages, *Sclerocephalus* was the top predator in its environment. ❒ *Amphibia, Limnarchia, Actinodontidae, Sclerocephalus haeuseri, postcranial morphology, ontogeny, Lower Permian, Germany.*

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Sclerocephalus is one of the best-known limnarchian amphibians in the Lower Permian of Central Europe. The type species, *S. haeuseri*, was described by Goldfuss (1847), but the holotype is lost (Boy, 1988). *Sclerocephalus* was described or referred to by several researchers (Ammon, 1889; Boy, 1976, 1988; Branco, 1887; Broili, 1908, 1926; Burmeister, 1850; Credner, 1893; Fritsch, 1901; Heyler, 1975; Meyer, 1857, 1858; Romer, 1947; Werneburg, 1983, 1989, 1992). Three known species are: *S. haeuseri* Goldfuss, 1847, *S. bavaricus* Branco, 1887 and *S. jogischneideri* Werneburg, 1992. Other species referred to *Sclerocephalus* do not belong to that taxon, e.g. *'S.' latirostris* Jordan, 1849 (= *Cheliderpeton latirostre* sensu Boy, 1993), *'S.' labyrinthicus* Geinitz, 1861 (= *Onchiodon labyrinthicus* sensu e.g. Watson, 1919) and *'S.' credneri* Fritsch, 1901 (= *Onchiodon labyrinthicus* sensu Werneburg, 1993 and *Capetus palustris* sensu Sequeira & Milner, 1993). On the other hand some larval individuals of *Sclerocephalus* where first misinterpreted and therefore described as or referred to other taxa. Romer (1939) first pointed out that *Branchiosaurus amblystomus* described by Credner (1882,1885, 1886, 1893) and Ammon (1889) belonged to *Sclerocephalus* (Credner's specimens are today assigned to *Onchiodon* (sensu Boy, 1990)). Later Boy (1972) recognised that *Leptorophus levis* Bulman, 1928 (= *Branchiosaurus levis* in Watson, 1963) and *Pelosaurus longiscutatus* Theobald, 1958 may represent larval individuals of *Sclerocephalus*.

Sclerocephalus had a wide palaeogeographical distribution (Werneburg, 1988) and is recorded throughout the Autunian. The oldest known species is *S. bavaricus* from the Altenglan Formation (Lower Autunian) of Ohmbach (Rheinland Pflalz, SW Germany). It is represented by only one incomplete skeleton (MB Am.442) with a well-preserved skull.

The type species *S. haeuseri* is best known and is represented by a large number of articulated skeletons, from the Saar-Nahe area in SW Germany (Rheinland Pfalz and the Saarland). Two subspecies were recognised by Boy (1988); *S. h. haeuseri* Goldfuss, 1847 and *S. h. jeckenbachensis* Boy, 1988. It is also the only species for which all ontogenetic stages are known.

New specimens, showing different ontogenetic stages, have been found during the last decade. They also provide new data concerning diet. This paper characterises the stages of ontogeny of *S. haeuseri* and discusses its autecology.

MATERIAL AND METHODS

MATERIAL. PMNB uncataloged, PMNB 393, larval individuals, complete skeleton with soft tissue preservation, length 8.5 and 9.5cm; GMS 307, larval individual, skull and pectoral girdle, skull length 16mm; PMNB 85, juvenile, complete skeleton with soft tissue preservation, length 13cm; PMNB 308, 177 juveniles, complete skeleton with soft tissue preservation, length 11 and 12.5cm; PMNB 179, juvenile, skull and parts of the pectoral girdle, skull length 18mm; GMS 24, juvenile, skull and parts of the pectoral girdle, skull length 25mm; GMS 228, 395, juveniles, complete skeleton with soft tissue preservation, length 14 and 24cm; GMS 394, juvenile, skull and anterior half of the body with soft tissue preservation, skull length 35mm; GMS 52, juvenile, complete skeleton with soft tissue preservation, length 30cm; PMNB 174, juvenile, almost complete skeleton with soft tissue preservation, length 22cm; GMS 396, PMNB 93, juvenile, complete skeleton with soft tissue preservation, length 26cm; PMNB 103, GMS 348, PMNB 415, GMS226, PMNB GRE-1, juveniles, complete skeleton with soft tissue preservation, length 25, 28, 29, 30, 48cm, respectively; PMNB uncatalogued, juvenile, complete skeleton with soft tissue preservation, length 26cm; PMNB PDC 327, adult, complete skeleton, length 74cm; PMNB BGC 69, adult, complete skeleton, length 72cm; PMNB BGC 112, adult, complete skeleton, length 79cm; BSPHG-1981 I99, adult, skull and partial skeleton, skull length 16cm, PMNB BGC 112, late adult, complete skeleton, length 182cm. GMS P/70, adult, isolated pelvis, length ca. 10cm. Private collection SKO, adult, complete skeleton, length 82cm.

REFERRED MATERIAL. About 800 coprolites from PMNB, GMS, GPIM and SKO.

LOCALITIES AND AGE. All larval and most of the juvenile specimens are from Rümmelbach/Gresaubach (Top L-O 10). One juvenile is from Gresaubach (PMNB GRE-1, Top L-O 10) and one from Wörsbach (PMNB uncataloged, Top L-O 10). Adults are from Niederhausen an der Appel (PMNB PDC 327, L-O 8), Jeckenbach (PMNB BGC 69, L-O 6), Odernheim (SKO uncataloged, L-O 6) and Raumbach (SKO no Nr., L-O 6). The oldest adult was found in Jeckenbach (PMNB BGC 112, L-O 6). The isolated pelvis was found in St. Wendel (GMS P/70, L-O 5). The coprolites are from horizons Q 1 to L-O 10. In general the collecting horizons are in the Lower Rotliegendes (Autunian of European stratigraphy sensu Boy & Fichter or Gzehlian/Asselian in global stratigraphy sensu Deitze, 2000).

METHODS. All specimens were drawn proportionally from radiographs. For smaller individuals a WILD M-3 binocular with camera lucida was used.

REPOSITORIES. BSPHG, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; PMNB, Pfalzmuseum für Naturkunde, Bad Dürkheim; GMS, Geologisches Museum der Saarberge AG, Saarbrücken; GPIM, Geologisch-Paläontologisches Institut, University of Mainz; MB, Museum für Naturkunde, Berlin; SKO, private collection Krätschmer, Odernheim.

ABBREVIATIONS. *Geological*. L-O, Lauterecken-Odernheim-Formation (current stratigraphy Lauterecken-Formation L-O 1 + L-O 2, Jeckenbach-Odernheim-Formation L-O 3 – L-O 10 (3 = lowermost/10 = uppermost). Q Quirnbach-Formation (Q1 = lower / Q2 = upper) (Dietze, 2000, fig. 1) *Anatomical*. Cl, clavicle; Cr, caudal rib; Ct, cleithrum; F, femur; Fi, fibula; H, humerus; I, interclavicle; Il, ilium; Is, ischium; Mc, metacarpus; P, pelvis; Ph, phalanges; Pu, processus uncinatus; R, radius; Sc, scapula; St, stomach contents; Ti, tibia; U, ulna; Va, ventral armour.

SYSTEMATIC PALAEONTOLOGY

AMPHIBIA Linnaeus, 1758
TEMNOSPONDYLI Zittel, 1888
LIMNARCHIA Yates & Warren, 2000
STEREOSPONDYLOMORPHA Yates & Warren, 2000
Superfamily ARCHEGOSAUROIDEA Meyer, 1857
FamilyACTINODONTIDAE Lydekker, 1885
Sclerocephalus Goldfuss, 1847

Sclerocephalus haeuseri Goldfuss, 1847

ADULT POSTCRANIAL. Vertebral column of 37-39 rhachitomous vertebrae (25 presacrals and 12-14 caudals). Neural arches high, robust, with those of the atlas-axis-complex only visible in older adults. Neural spine of the fourth cervical vertebra somewhat shorter; feature of other temnospondyls such as *Eryops* (Moulton, 1974) and *Balanerpeton* (Milner & Sequeira, 1994). Transverse processes short but prominent, posteroaterally directed, with large, vertical diapophyses. Pre- and postzygapophyses well-developed and about equal in size.

Proximal articulation surface of ribs relatively broad, because of coossification of the capitulum and tuberculum. Ribs 2-14 with a prominent processus uncinatus close to their posterior margin (Fig. 5). These processus hook-like, contacting the anterior margin of the following rib. Ribs 2-4 longest. Following ribs taper

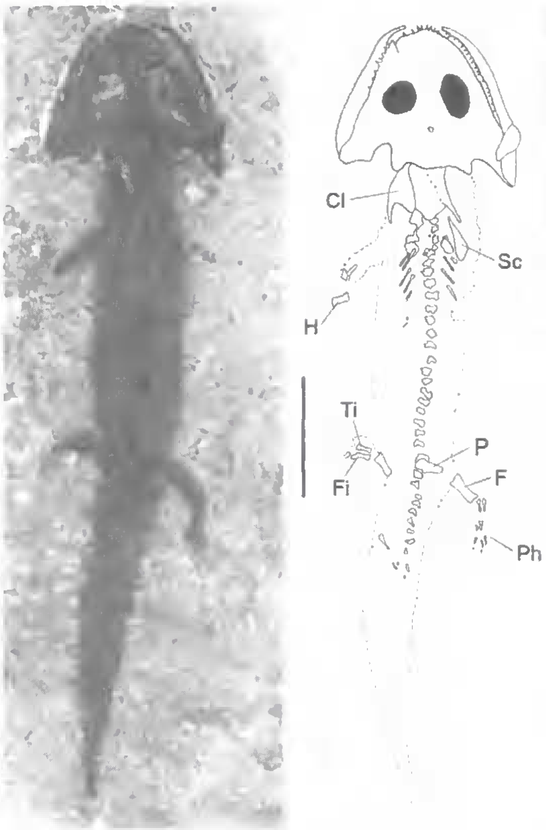

FIG. 1. Larval individual (PMNB uncataloged) in dorsal view. Scale-bar = 1cm.

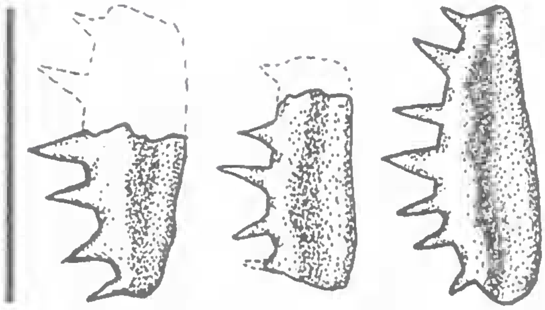

FIG. 2. Gill-teeth ('Kiemenzähne'), which were attached at the ceratobranchial filaments. Scale-bar = 1mm

slightly in length back to 14-15 vertebra and then rapidly to the pelvis. Shoulder girdle of interclavicle (which is the central ventral element) and paired clavicles, scapulocoracoid and cleithrum. Interclavicle a relatively flat bone of rhombic shape; ventral surface with numerous cristae and furrows, running from the edges to the centre. Clavicles flat, triangular, medially curved in their ventral section, broadly contact the interclavicle; dorsal process with posteriorly directed tip contacting the ventral process of the cleithra; ventrolateral margin also with some furrows. Scapulocoracoids the most prominent bones of the shoulder girdle. Shoulder blade formed as a broad, posteromedially directed, dorsal process, articulating with the clavicle anteroventrally and with the cleithrum anterodorsally. Coracoid part of the scapulocoracoid ventrally on the posteroventral margin. Prominent glenoid surface in the posterior margin. Large supraglenoid foramen above the glenoid surface. Cleithra flat, arch-shaped, of triangular outline, contacting the scapula blade with their posteromedial margin, running ventrally out in a sharp process meeting the dorsal process of the clavicle in about the anterior mid-section of the scapula blade.

Humerus robust, moderately elongated, with tetrahedal shape (Meckert, 1993 sensu Romer, 1939) similar to the humerus of *Eryops* (Miner, 1925);.proximal head prominently convex, above the processus latissiumus dorsi and the crista pectoralis posteriorly and the crista dorsalis anteriorly; distal surface anteroposteriorly expanded, bearing a relatively small processus supinator and somewhat larger ectepicondylus anteriorly, as well as a very prominent entepicondylus posteriorly.

Radius and ulna relatively short elements; radius more robust, with slightly widened ends, with concave shaft; ulna more slender, with proximal part bearing the olecranom widened somewhat medially directed; olecranom very prominent, only fully ossified in older adults.

Manus well ossified in older adults, described in detail by Meckert, 1993. Phalangeal formula 2/2/3/3. On the ventral part of the body, between the interclavicle and the pelvis, there is a compact ventral armour of epidermal scales. Boy (1988) and Broili (1926) described this armour in detail. Scales generally long and sharp in the midsection and oval or circular laterally. At the level of the forelimbs, there is a prominent recess on each side of the armour. Ossification of these scales had already started in the late larval stage, in individuals with a skull length of approximately 20mm (Boy & Sues, 2000).

Pelvis very robust; ilium its most prominent element; ventral part fan-shaped anteroposteriorly bearing most of the acetabulum; dorsal part elongate-rectangular, curved posteriorly.

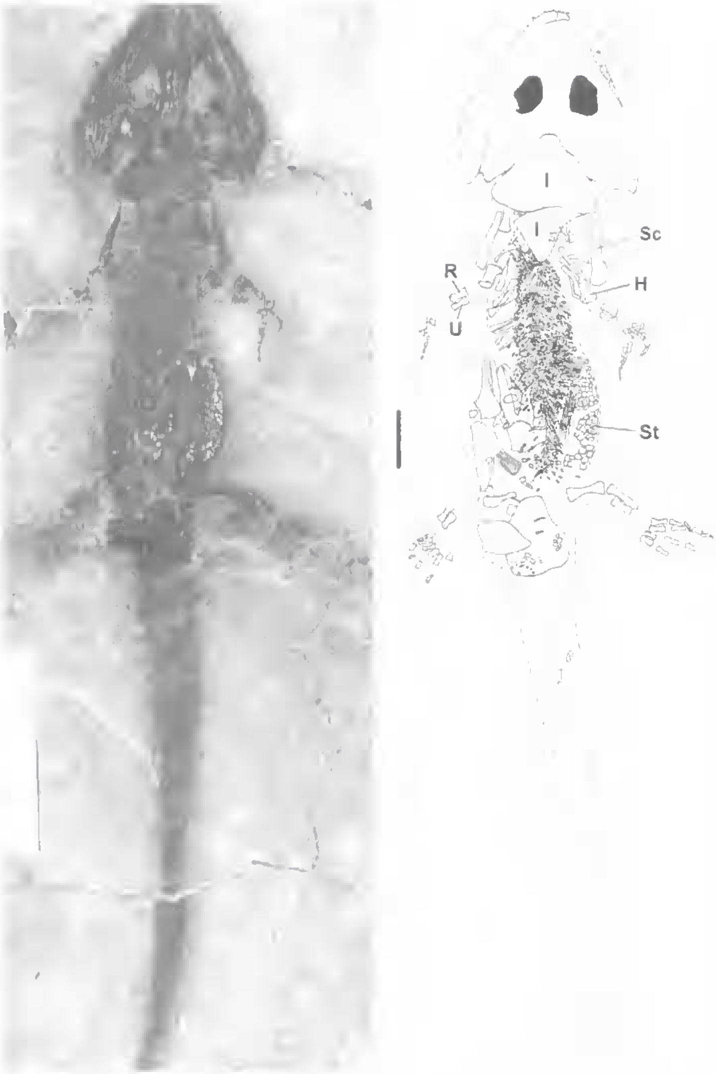

FIG. 3. Juvenile individual (PMNB uncataloged) in ventral view. In this specimen, scales of paramblypterids are visible as stomach contents (St). Scale-bar=1cm.

The ventral section of the pelvic-girdle consists of the pubis and ischium, which together represent a somewhat triangular shaped plate. Hind-limbs well-developed in adults. Femur massive, rectangular, clearly the largest element of the limbs; proximal end broadened and somewhat more prominent than the distal one. Fourth trochanter weakly developed, situated proximally, with distal half of shaft still robust, terminating in a relatively straight articulation surface. Tibia and fibula much shorter than the femur; fibula somewhat shorter than tibia. Tibia less robust, with slender distal portion, contacting the tibiale ventrally and the intermedium medially. Fibula massive, with expanded distal end with a medially directed tip. This tip touching the intermedium, while the medial margin contacts the fibulare. Metatarsals only visible in older adults. Tibiale, intermedium and fibulare very well-developed. Tibiale triangular, situated laterally, smallest of proximal metacarpals. Intermedium oval, between tibiale and fibulare; fibulare situated medially, very prominent, roughly triangular. Phalanges rod-like, terminate in a claw-shaped phalanx. Phalangeal formula varies between 2/2/3/3/3 and 2/2/2/3/3.

ONTOGENY

Four ontogenetic stages (larval, juvenile, adult and late adult) are characterised by features of the postcranial skeleton. The pectoral girdle has already been described by Meckert (1993) and the cranium by Boy (1988).

LARVAL STAGE (skull length 0.8-2.5cm). The basis for larval anatomy is an 8cm long specimen (PMNB uncataloged) (Fig.1) with well-preserved body outlines and carbonaceous imprints of the external gill. The basibranchiale was probably cartilaginous. It ossifies in the juvenile stage and is prominently developed in adults (Boy, 1972, 1988; Boy & Sues, 2000). The ceratobranchials were arranged in up to 4 rows and situated laterally at the level of the shoulder girdle. They probably also consisted of cartilage, but had attached to them small bony plates, so-called gill-teeth ('Kiemenzähne' after Boy, 1972) (Fig. 2). Each gill-tooth had approximately 5 spine-like denticles, which vary by 1-2 spines. Similar structures are known in *Micromelerpeton* (Boy, 1995) and *Gerrothorax* (Nilsson, 1946). The hypobranchials, hypohyals and ceratohyals were not preserved.

The limbs are conspicuous but only slightly ossified in the Bad Dürkheim specimen. The humerus is very short and nearly quadratic; the radius and ulna are weakly developed, but the radius is longer. Elements of the manus are not recorded and were probably cartilaginous. The femur is rectangular in lateral view, relatively short, very robust and longer than the less developed tibia and fibula. Elements of the pes are badly preserved. The centra are rhachitomous and bear paired neural arches with low neural spines (Boy, 1972). Ribs of vertebrae 1-14 are ossified, rod-like and slightly broadened proximally. Capitulum and tuberculum not clearly developed. The sacral rib is slender. Caudal ribs have not been recorded. The pelvis is relatively weak and not as robust as the well-developed shoulder-girdle (Meckert, 1993). The tail occupies approximately 50% of body length. No stomach contents could be found.

JUVENILE STAGE (skull length 3.5-7.5cm). Representative juvenile is a 26cm long specimen with clearly visible body-outlines (PMNB uncataloged) (Fig. 3). The external gill has been lost and limbs are more ossified. The humerus shows no major differences to that in the larval stage. Radius and ulna are about as long as the humerus. Radius and ulna are approximately equal in length, but the radius is somewhat more robust. The femur is elongate-rectangular with slightly expanded proximal and distal ends. It is clearly more robust and about twice as large as the tibia and fibula. The tibia is rod-shaped and slightly expanded distally. The metapodials are not ossified; phalanges are clearly visible. Claw-like terminal phalanges are developed. GMS 394 shows that the vertebrae are well-ossified and bear lower neural arches and spines as in adults. The ribs are more robust than in the larval individual. The 2nd to 14th presacral ribs are club-like and broadened laterally. Between 12 and 14 caudal ribs are presented. The second and third ribs, distal to the sacral rib, are longest. The tail occupies about 45% of body length, but is shorter than in larval individuals.

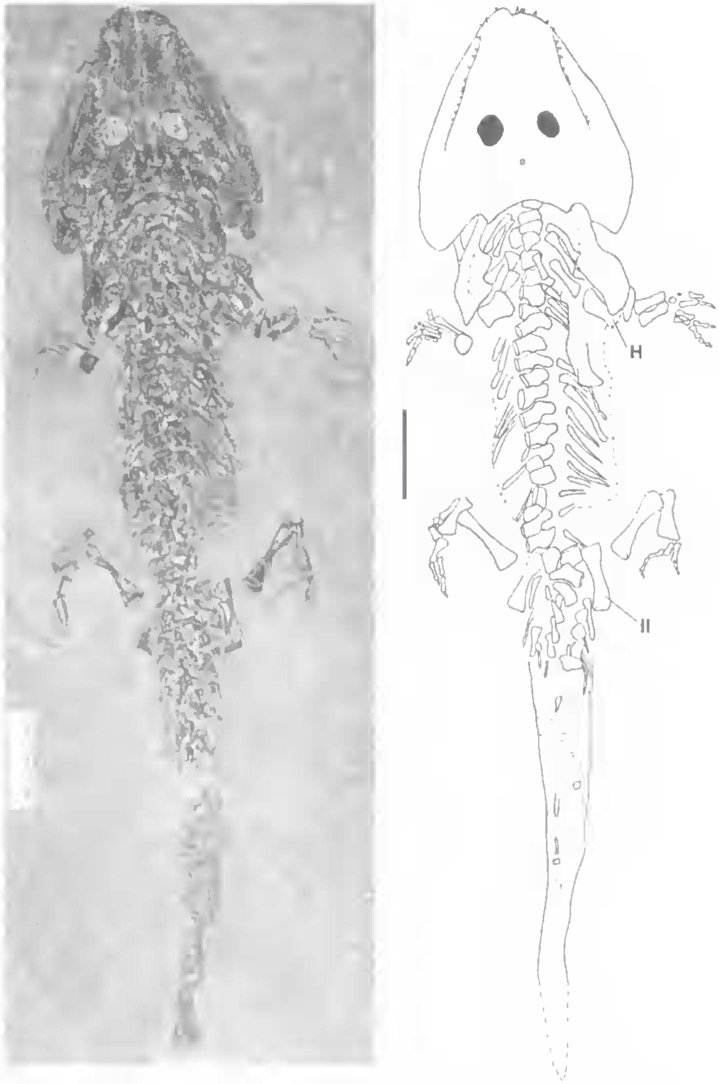

FIG. 4. Adult individual (PMNB PDC-327) in dorsal view. Scale-bar = 5cm.

ADULT STAGE (skull length 9.5-16cm). The representative adult is a well-preserved skeleton 74cm long (PMNB-PDC 327) (Fig. 4). In general, the body has become somewhat more compact. The humerus is robust, but not as stout as in juveniles. Its proximal and distal ends are still cartilaginous (Broili, 1926; Boy, 1988). Ulna and radius are about equal in length, but the radius is more robust. In both, the shaft is inwardly curved, with the ulna showing a more prominent inflexion.Phalanges are broader than

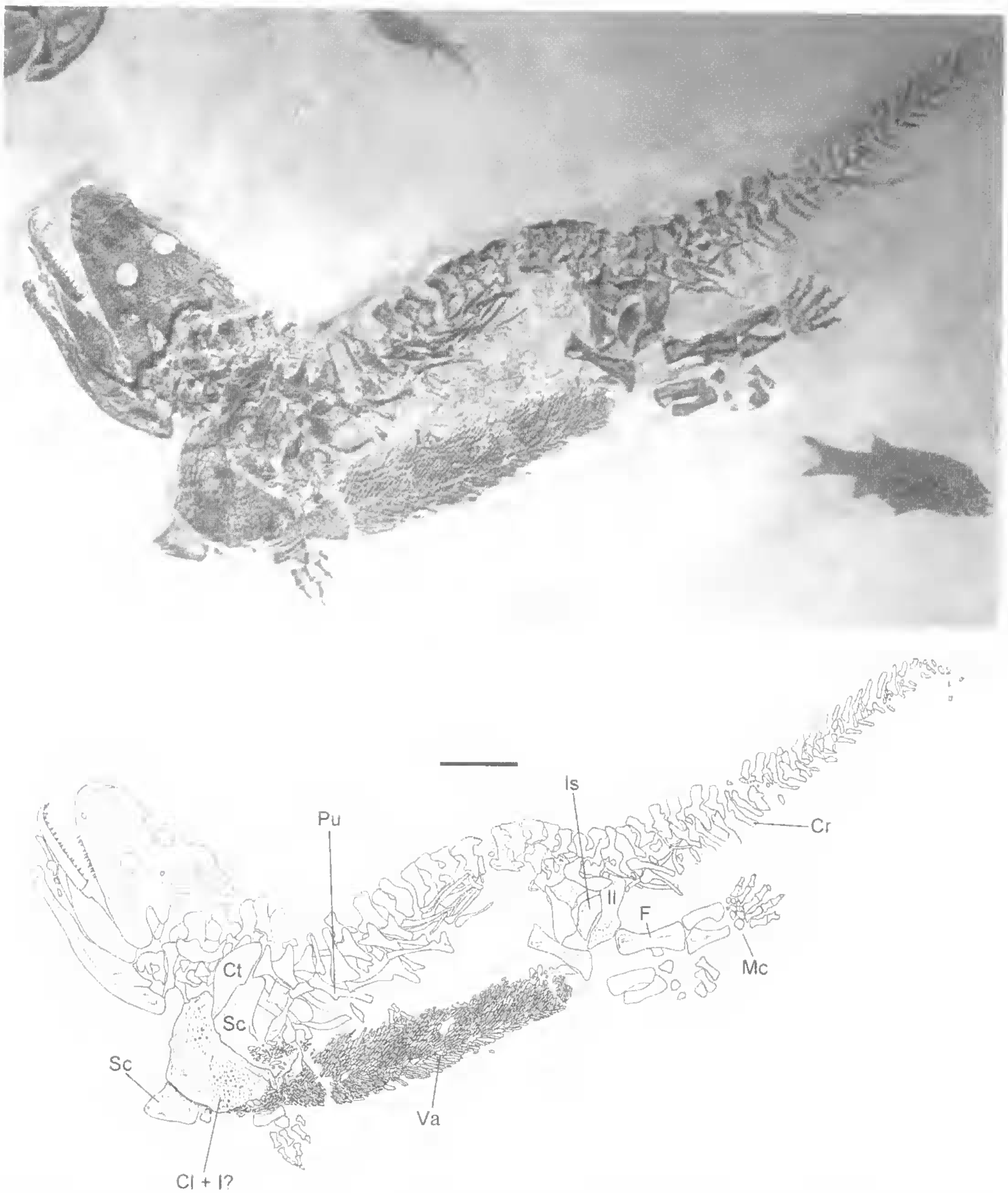

FIG. 5. Late adult individual (PMNB BGC-112) in lateral view. In this stage the ventral armour (Va) is clearly visible. Scale-bar = 20cm.

in juveniles and still not completely ossified. Also the metacarpus is not completely ossified. The hind-limb elements are similar in shape to those in the juvenile specimens, but are more robust. Metatarsals are present.

Vertebrae are well-developed. The pleurocentra are slender and of rhachitomous shape (Schoch, 1999: 107). Boy (1988) described the intercentra as unpaired with a low semicircular shape and the neural arches as robust and

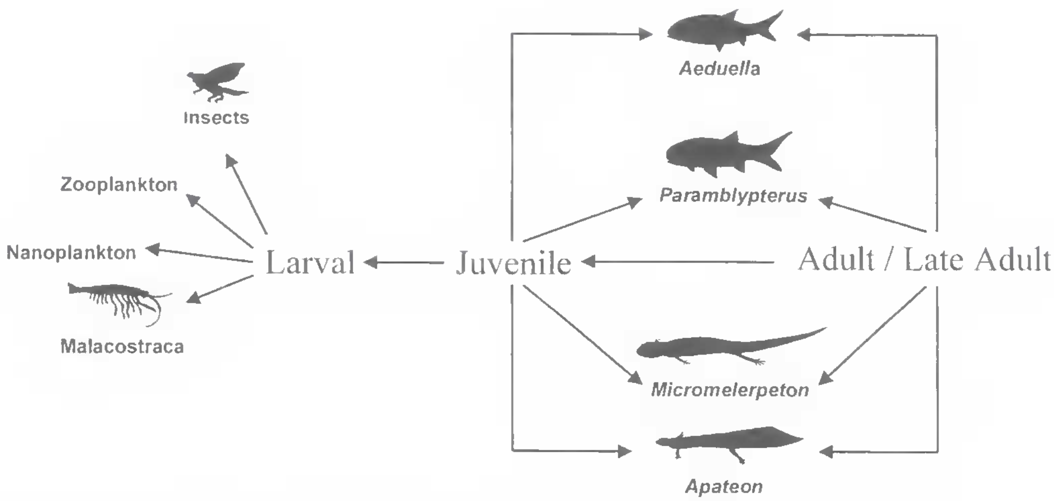

FIG. 6. Proposed food chain of *Sclerocephalus* in the larval, juvenile and adult/late adult stage.

relatively high. This could also be observed on PMNB-PDC 327.

All ribs are strongly developed and have a co-ossified capitulum and tuberculum. This is especially visible in ribs 2-14 where the proximal ends are broadened into a club-like shape. These ribs bear a hook-like processus uncinatus posteriorly. In large individuals, there are lateral depressions on ribs 2-6. Pelvic- and shoulder-girdles are robust and the pelvis is now completely ossified. The tail is shorter than in juveniles. It occupies about 40% of body-length.

LATE ADULT STAGE (skull length >18cm). The late adult stage is based on PMNB-BGC 112 (Fig. 5). In general the body is shorter than in earlier stages and all bones are well ossified. Humeri are robust and slightly elongated. Metapodials are completely ossified. Of the atlas-axis-complex only the neural arches are visible. Tuberosities on the proximal ends of the ribs change from being club- to bow-shaped and can be observed to rib 7 (but possibly extended to 9). Also the lateral depressions, mentioned for the adults, can be recorded to ribs 7-9, and are deeper. The pelvis is extremely robust. The tail is shorter then in earlier stages, but does not differ much from that of adults (it also occupies 40% of body-length).

HABITAT RECONSTRUCTION

During the Lower Permian, the Saar-Nahe Basin in SW Germany was traversed by several river systems. In some areas water was trapped in low relief, forming lakes (Dietze, 1999). These lakes (Table 1) normally existed only for a relatively short geological period, but contained a well-balanced ecosystem (palaeocommunities after Boy, 1998 sensu Järvinnen et al., 1986), composed of large amphibians (e.g. the limnachian *Archegosaurus*), small amphibians (e.g. the branchiosaurs *Micromelerpeton* and *Apateon*), large fishes (e.g. the xenacanthodian freshwater sharks *Xenacanthus* and *Orthacanthus*), small fishes (e.g. the amblypterid *Paramblypterus* or the acanthodian *Acanthodes*), as well as a variety of different invertebrates (e.g. ostracods, bivalves, shrimps) (Boy, 1998). One of the larger lakes was Lake Humberg (L-O 10) that extended over an area of 3,400km^2 and deposited nearly the whole Saar-Nahe Basin (Stapf, 1990). Boy (1994) mentioned, that lake deposits from Lake Humberg can be divided into 4 phases.

TABLE 1. Distribution of the ontogenetic stages of *Sclerocephalus haeuseri* in different lake localities (primary based on unpublished excavation reports of the Pfalzmuseum für Naturkunde, Bad Dürkheim).

Layer	Lake	Lake-size (km^2)	Larval	Juv.	Adult	Late Adult
L-O 10	Rümmelbach - Humberg	ca. 3400	14	ca.100	0	0
L-O 9	Ruthweiler	ca. 10	?1	0	0	0
L-O 8	Odernheim	ca. 760	31	ca.100	2	0
L-O 7	Jeckenbach-Heimkirchen	ca. 230	0	4	ca.50	8
L-O 6	Niederkirchen	ca. 40	0	2	2	2
Q 2	Quirnbach	ca. 500	0	0	0	1
Q1	St Wendel	ca. 40	0	2	20	3

Sclerocephalus is found (together with *Paramblypterus uvernoyi* and *Apateon pedestris*) only in the first phase, when the Lake was deepest. In other lakes, such as in Lake Odernheim (L-O 8), *Sclerocephalus* was found together with the large branchiosaur *Micromelerpeton* (Boy, 1994) or with the small freshwater shark *Triodus* (Lake Klauswald, L-O 9, after Dietze, 1999).

Boy (1988) concluded that juvenile *Sclerocephalus* individuals might have lived in shallow lakes. We suggest that juvenile *Sclerocephalus* lived in large, relatively deep lakes of the Rümmelbach-Humberg type. Recent extensive excavations by the Pfalzmuseum für Naturkunde in Bad Dürkheim in the corresponding localities Gresaubach/Lebach and Humberg/Odernheim (Top L-O 10) support this suggestion as only larval and juvenile individuals have been found. It therefore is suggested that these lakes were being used as spawning grounds whilst adult individuals lived in another environment. Also, this could explain why, in lakes where adult and late adult individuals are common, as in Lake Jeckenbach (L-O 6) (Stapf, 1990), larval and juvenile individuals are rare or absent.

DIET DURING ONTOGENY

As mentioned above, no stomach contents could be associated with the larval specimens. Most probably their diet consisted of plankton and malacostracans (as the common *Uronectes*) or maybe small insects. Boy (1993) suggested that larval *Sclerocephalus*, similar to some recent amphibians could have caught its prey with a suck-snap method (Bramble & Wake, 1985). Juveniles caught large prey. As mentioned above, a complete, large *Paramblypterus* with its head folded backwards was found in the stomach of PMNB (uncataloged). Altogether 6 fish-bearing specimens were observed (only one in a public collection, PMNB, uncataloged, fig. 3); another one (GPIM-N 1166) was mentioned by Boy (1988). We therefore conclude that *Sclerocephalus* swallowed these fishes whole. In numerous specimens, scales of paramblypterids, and also traces of small amphibians such as *Apateon* and *Micromelerpeton*, have been found. As a rarity, the stomach of 1 specimen (GMS, uncataloged) contained remains of a smaller *Sclerocephalus*. This is the first record of cannibalism in this taxon.

Adult and late adult individuals were primary piscivores, in which *Paramblypterus* represents the common prey. Observations of stomach contents and a large number of coprolites showed that smaller amphibians and probably smaller *Sclerocephalus* individuals also belonged to the prey. Acanthodians were never present as stomach contents or in the coprolites. These fishes were very common in the environment of *Sclerocephalus* and of moderate size, but had large spines anterior to their fins. It is possible that the more heavily built adult and late adult *Sclerocephalus* individuals mostly did not hunt actively, but watched for prey next to the shore and caught them with the suck-snap method. If we accept this premise, *Paramblypterus* and small amphibians would have been an easier prey than the spine-bearing acanthodians.

CONCLUSIONS

In the first ontogenetic phases, *Sclerocephalus haeuseri* was well adapted to its aquatic habit,

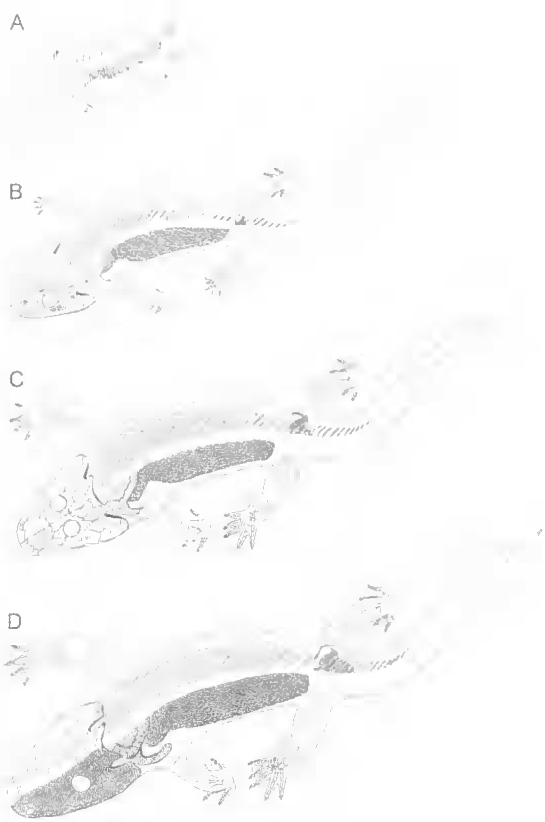

FIG. 7. Idealised reconstruction of the four ontogenetic stages: A, larval; B, juvenile; C, adult; and D, late adult. The right side of the body shows the dorsal bones, the left side shows the ventral elements.

which is especially perceptible in the slender shape of the body, the weakly ossified limbs and the long rudder-tail. Larval individuals are up to 10cm in length. Their jaws were not very strong and bore only slightly developed teeth (Boy, 1988); therefore their diet must have consisted of plankton and probably insects or malacostracans.

In the juvenile stage, individuals could reach to 50cm long. They still had a slender body-shape and a long tail and probably were active hunters. Stomach contents and coprolites contain remains of paramblypterids and small amphibians, including smaller individuals of *Sclerocephalus*. The prey was swallowed entirely. It is conspicuous that some lakes, especially those of the 'Rümmelbach-Humberg-Lake' type, nearly exclusively yielded larval and juvenile individuals (up to the late juvenile stage (= late 'metamorphic' stage after Boy & Sues, 2000) or subadult stage (Table 1). We therefore conclude that adult *S. haeuseri* might have changed their habit from fully aquatic to amphibious. Adults probably visited the habitat of the younger ones to spawn; therefore they are rarely recorded in these layers. According to Boy (1998) both juvenile and adult / late adult individuals were the so-called top-predators in their environment (Fig. 6). In Lake Niederkirchen *Sclerocephalus* shared this position with the freshwater shark *Orthacanthus senckenbergensis*. In Lake Humberg, as mentioned above, *Sclerocephalus* was only recorded in the first of 4 phases. In the second phase the position as top-predator was held by the freshwater shark *Xenacanthus meisenheimensis* (Boy, 1994), while in the fourth phase the top-predator position was shared by the archegosaurids *Archegosaurus* and *Cheliderpeton*. The latter is the closest relative to *Sclerocephalus* (Yates & Warren, 2000) and is also known in different ontogenetic stages (Boy, 1993; Steyer, 2000).

In the adult/late adult stage, *Sclerocephalus* specialised on paramblypterids, but also caught smaller amphibians such as *Apateon* or *Micromelerpeton*. Although *Acanthodes* was very common in the lakes, it was not recorded in the stomach contents or coprolites and therefore probably was not preyed upon. The limbs were well ossified in the adult stage, so that these individuals also could have been terrestrial from time to time.

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